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[From the American Naturalist, Vol. V, October, 1871.]

EXPERIMENTS WITH VIBRATING CILIA.

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THE motions of vibrating cilia, and their action on the water around them, are among the most beautiful sights shown by the microscope. They are best seen on the respiratory surfaces of both land and aquatic animals, and of the last, the gills of the Mytili are especially favorable for examination. In such cases, the effects are confined to the movement of the secreted mucus, or of the surrounding water, and the particles floating in it, while in others the cilia cover the outer surface and become the chief organs of locomotion, as in the Infusoria. In the eggs of Radiates and Molluscs, as in the remarkable phenomenon of the rotation of the yolk, much larger masses are moved, and among Batrachians, the yolk, soon after impregnation and segmentation, being large enough to be easily watched with the naked eye, is seen to revolve steadily under ciliary influence. Even the recently hatched larvæ of frogs and toads are carried along bodily by the same agents distributed over the whole outward surface, without the slightest aid from the muscular system. In all of these instances, however, although in some the mass moved is considerable, the motion takes place in a fluid, of nearly the same specific gravity as the objects, and so the force required to give the motion is exceedingly small. Indeed everything serves to give the impression that cilia are capable of exerting only the

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most delicate efforts. There are several ways in which their effects may be shown without the aid of the microscope, but the most common is that of sprinkling some light powder over the ciliated membrane, from which the powder is soon swept away. The object of this paper is to explain some other methods adapted to class experiments having the same end in view, but by which motion is imparted to much larger masses, and also to show that in some instances a much greater resistance can be overcome than has generally been supposed possible.

I. *Experiments in water.* — For these the gills of *Unios* and *Anodontas* are well suited. Their cilia are quite active, and vibrate in such directions, that on the inner gill the motion is *from* the free edge, and on the outer *to* it, facts which the experimenter should keep in mind. If an *inner* gill is cut away from its attachment and laid on the bottom of a flat dish, its cilia acting as legs, it will soon begin to move with its *free* edge forwards, and will in the course of time, travel the entire length of the dish. We have seen a whole gill move ten inches in four hours. Under similar circumstances the *outer* gill will move with its base or *cut* edge forwards. This difference depends, as will be readily seen, upon the fact that the cilia of the two gills vibrate in opposite directions.

The result of ten experiments gave the rate of motion of a piece of gill measuring 12mm. by 14mm., 6mm. a minute. If two outer gills are laid with their free edges towards each other they will at once begin to approach, and it frequently happens after meeting that one crawls directly over the other.

Another and more striking experiment which shows the reaction of cilia on each other may be made as follows. Fasten a gill to a piece of cork under water, and place upon it a portion of a second gill about a half inch square. If this piece is so placed that the cilia vibrate in the same direction with those of the gill below, it will remain stationary, or nearly so, since the cilia offer no resistance to each other. If now the upper piece is reversed so that the cilia vibrate in opposite directions, the upper piece will move with double the speed and through twice the distance in a given time that it would with its own cilia alone, for while the lower cilia move the upper piece through a certain space, the cilia of the upper piece also move this in addition through an equal space. A third form of this experiment consists in placing the upper piece so that its cilia vibrate at right angles to those of the lower. In this case, while the lower cilia tend to move the upper

piece from side to side, those of the upper tend to move this lengthwise of the lower. The direction which the upper piece takes, is a resultant one, viz., intermediate between the two.

II. *Experiments in air.* Though the tissues of the gills of *Unios* and *Anodontas* are quite soft and incapable of resisting other than very light weights, they will nevertheless carry small discs of paper supporting a bristle, on the top of which is a small pellet of cotton or a flag of tissue paper. In order to show the flag more distinctly, a board painted black should be nailed to the edge of the one on which the gill rests, to make a back ground. With this precaution the experiment may be seen over a large room. To mark the distance traversed, a pointer of white paper should be set up on the board supporting the gill and at the beginning of the experiment, the end of the pointer brought in contact with the end of the flag on the gill. When left to itself, the disc on the gill with its flag at once begins to move to the opposite side and the flag is seen to recede from the pointer. The distance traversed may be increased to several inches, by placing two or more gills side by side, the free edge of the first slightly overlapping the cut edge of the second, etc.

The mucous membrane from the roof of the mouth of frogs, is much more solid than the gills of *Unios*, and the cilia vibrate with much greater force. Different ciliated membranes exert very different degrees of force, but we have found none better suited for experiments than that just mentioned; especially, when taken from the mouth of the bull frog which gives a large surface. It has the advantage, too, of keeping up its activity for twenty-four hours or more, after being detached from its natural connections, if only kept cool and moist. For moistening it water answers sufficiently well, but the serum of the blood of the frog is still better.

The attention of the writer was first called to the possibility of moving weights much larger than was supposed possible by noticing the ease with which a piece of skin which was accidentally placed upon the ciliated membrane was swept off. By loading the piece of skin with weights the mass moved was found to be unexpectedly large.

In making experiments for the purpose just mentioned we have adopted the following method. The mucous membrane, being carefully dissected from the roof of the mouth, is pinned to a board. A piece of skin from near the throat of the frog, and

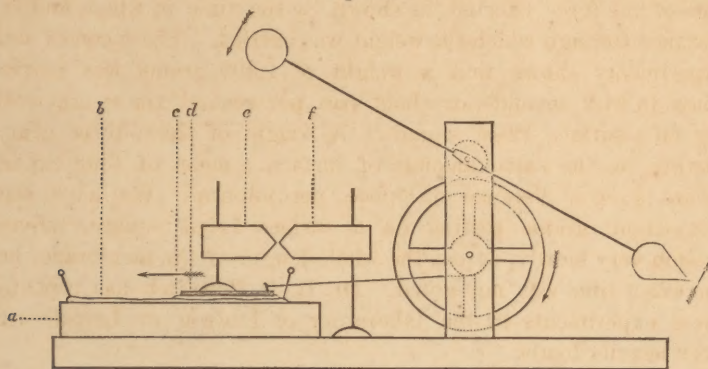
from one-third to half an inch square, is placed upon this membrane with the inner surface in contact with the cilia, it being kept in mind that these vibrate from before backwards towards the throat. On the skin may be placed a plate of lead of somewhat smaller size. This serves as a vehicle to which weights may be added at will to increase the load, and also as a drag, to set in motion the instrument described farther on. To show the distance through which the load is carried, the flag and pointer may be used as in the case of the gills before described. Pains should be taken to have the board on which the experiment is made perfectly horizontal, otherwise a sliding motion, especially when heavy weights are used, may come in to vitiate the experiment.

Although the results are not uniform, the following will give some idea of the force exerted, as shown by the time in which and the distance through which the weight was carried. The mean of four experiments shows that a weight of 1.300 grams was carried 15mm. in 61.2 seconds, or about 4mm. per second, the weight resting on a surface 12mm. square. A weight of thirty-three grams resting on the same amount of surface, a mean of four experiments gave a distance of 6.6mm. per minute. We have seen forty-eight grams resting on a surface 14mm. square, moved, though very slowly, across the whole length of the membrane, but the exact time was not noted. Dr. H. P. Bowditch has repeated these experiments in the laboratory of Ludwig at Leipsic with even heavier loads.

Finding that so much force was exerted, the idea of utilizing it was naturally suggested, and after various trials the following instrument was devised for this purpose, in which the direct motion produced by the cilia was made to give rise to a rotary one. The instrument consists of two light toothed wheels (see figure), the larger 30mm. and the smaller 5mm. in diameter. To the axis of the first is attached a small drum 5mm. in diameter, around which is coiled a thread of the finest and most flexible cotton. The axis of the smaller wheel is prolonged through the frame in which both wheels move, and carries on its end an index made of two bristles inserted into a central piece of cork, which is attached to the axis. On the end of each bristle is a very light paper pointer. The whole length of the index is 110mm. but may be made longer or shorter than this, as may be convenient to the experimenter. Behind the instrument there should be a small black board attached to the base on which the frame rests, to serve as a back-

five ground against which the pointers are seen. The instrument is of sufficient delicacy to be moved by a weight of from ~~one~~ ^{five} hundred to ~~one~~ hundred and twenty millegrams or of from seven to eight grains. All that is necessary to make an experiment is to attach the end of the thread coiled around the drum to the hook on the lead which rests on the piece of skin, which in turn rests on the membrane. The proportions of the wheels are such, that when the load resting on the membrane is carried through a space of 7mm. the index makes two whole revolutions, and the point of the index moves through a space of about two feet. One complete revolution is effected in about thirty seconds. This motion may be easily seen over a large lecture room.

Fig. 110.



Description of the diagram. *a.* A movable block of wood to which the ciliated membrane is pinned. *b.* Ciliated membrane. *c.* Piece of skin resting upon it. *d.* Plate of lead with a small hook to which the thread coiled around the drum is attached. *e.* and *f.* Pointers, one resting on the lead and the other on the board to which the instrument is fastened; these are made of wire inserted into a base of wood or cork, and carry each a piece of paper or thin card; both are movable. The wheels are toothed. Attached to the axis of the large wheel is the drum, and to the projecting portion of the axis of the small wheel is the index.

This figure is one-half the size of the instrument. The base on which the instrument rests, should be made longer than in the figure so that the block to which the membrane is attached may be farther off from the wheels.

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